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EDAPHIC SPECIALIZATION IN THE CRYPTIC SPECIES *MENTZELIA MONOENSIS* (LOASACEAE)

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Abstract

Mentzelia monoensis J. M. Brokaw & L. Hufford is a cryptic hexaploid species known only from Mono County, California. Previous studies have suggested a recent allopolyploid origin of *M. monoensis* but have not investigated the causes of its narrow distribution. Here we report the discovery of a unique haplotype from the chloroplast intergenic spacer *ndhF-rpl32* that is sufficient to distinguish *M. monoensis* from all other species in *Mentzelia* sect. *Trachyphytum* using preserved specimens from any developmental stage. Based on soils collected with verified voucher specimens, we show that the edaphic niche of *M. monoensis* is significantly different from those of all other species in *Mentzelia* sect. *Trachyphytum*. A principal components analysis suggests the edaphic niche of *M. monoensis* is also one of the most extreme in *Mentzelia* sect. *Trachyphytum*. Most populations of *M. monoensis* were collected in soils derived from silica-rich rhyolite tephra produced by the Mono Craters volcanic chain. These coarse textured soils are lower in cation exchange capacity and plant available nutrients than those of any other species in *Trachyphytum*. Our findings suggest that edaphic specialization may have played a significant role in the establishment and geographic distribution of *M. monoensis* and other species in the Mono Basin.

Key Words: Cryptic species, edaphic, endemic, evolution, *Mentzelia*, Mono Craters, polyploidy, rhyolite, specialization.

Mentzelia monoensis J. M. Brokaw & L. Hufford is the most recently described species in *Mentzelia* sect. *Trachyphytum* Torr. & A. Gray, a monophyletic group comprised of roughly 20–30 annual species occurring primarily in western North America (Darlington 1934; Zavortink 1966; Hufford et al. 2003; Brokaw and Hufford 2010a, b, 2011). *Mentzelia* sect. *Trachyphytum* is unique among sections of *Mentzelia* L. for its high number (approximately 2/3 of the named taxa) of polyploid species (Zavortink 1966). *M. monoensis* is hexaploid with a hybrid origin from the progenitors *M. montana* (Davidson) Davidson (tetraploid) and *M. dispersa* S. Watson (diploid or tetraploid) (Brokaw and Hufford 2010b). Most polyploids in *Mentzelia* sect. *Trachyphytum* may be generally characterized as either widespread ruderals or narrowly distributed edaphic specialists (Brokaw 2009). However, *M. monoensis* occurs in both disturbed sites and barren pumice flats in the Long Valley Volcanic Field near Mono Lake, California (Brokaw and Hufford 2011). *Mentzelia monoensis* is thought to be endemic to Mono County (Brokaw and Hufford 2011), and the California Native Plant Society has recently listed *M. monoensis* as a California Rare Plant Rank 4 (plants of limited distribution), which indicates potential for future vulnerability (CNPS 2014). In order to better understand the conservation needs and evolutionary potential of *M. monoensis*, it is necessary to investigate the causes of its narrow distribution.

Considerable attention has been given to the occurrence and causes of rare and endemic species for purposes of both conservation and evolutionary theory (Stebbins 1942; Stebbins and Major 1965; Stebbins 1980; Myers et al. 2000). Although the investigation of endemics is critical to the recognition of general evolutionary trends (Burge and Manos 2011), the distributions of individual species may be determined by unique combinations of historical, genetic, and environmental factors (Stebbins 1980). Historical explanations of endemism have distinguished paleoendemics (relictual endemics that have usually experienced decreases in range size due to environmental change) from neoendemics (recently derived lineages that have never had substantially larger distributions) (Stebbins and Major 1965; Raven and Axelrod 1978). Although the *Mentzelia* sect. *Trachyphytum* crown group is estimated to have diverged 0.8214 (95% CI: 0.09–4.91) million years ago (Schenk and Hufford 2010), it has been suggested that *M. monoensis* and one of its progenitors, *M. montana*, have very recent origins within *Mentzelia* sect. *Trachyphytum* (Brokaw and Hufford 2010b). Thus, as the descendant of a young progenitor, *M. monoensis* is one of the youngest species in a relatively young lineage and is likely best described as a neoendemic both in terms of age and historical distribution. Explanations of limited distribution in neoendemics have included 1) insufficient time for dispersal (Willis 1922), 2) gene pool depletion by genetic drift (Stebbins 1942), and 3) habitat

specialization during speciation (Lewis 1966; Grant 1981). Observations based on the earliest discovered populations of *M. monoensis* have suggested that it is associated with unusual substrates derived from the Mono Craters volcanic chain (Brokaw 2009; Brokaw and Hufford 2011). In this study we focus on characterization of these edaphic conditions in order to test the hypothesis that habitat specialization explains the narrow distribution of *M. monoensis*.

The Long Valley Volcanic Field has experienced abundant volcanic activity for over three million years with some of the most recent eruptions forming the Mono Craters 40,000 to 600 yr ago (Bailey 2004; Riley et al. 2012). Holocene deposits from the Mono Craters are primarily composed of high-silica rhyolite, and these eruptions have left layers of pyroclastic rhyolite to depths of up to two meters throughout the Mono Basin (Bailey 2004; Hildreth 2004; Riley et al. 2012; Bursik et al. 2014). These substrates are potentially stressful habitats for plants because rhyolite weathers more slowly and has lower concentrations of plant-essential elements, including Ca, Fe, and Mg, than igneous rocks with lower silica contents such as basalt (Wolff-Boenisch et al. 2004, 2006; Olsson-Francis et al. 2012). Further, other Mono County endemics, including *Astragalus monoensis* Barneby and *Lupinus duranii* Eastw., are known to be associated with these coarse volcanic soils (Sugden 1985), suggesting edaphic specialization.

Another possible explanation for apparent endemism is our inability to identify *M. monoensis* outside of its known range. This potential deficiency can be attributed to both the short amount of time that *M. monoensis* has existed as a described taxon (Brokaw and Hufford 2011) and the difficulty in distinguishing the species from others in *Mentzelia* sect. *Trachyphytum* (Brokaw and Hufford 2011). Morphologically, *M. monoensis* is difficult to identify because it closely resembles other allopolyploid species in *Mentzelia* sect. *Trachyphytum* with overlapping character states. *Mentzelia monoensis* can usually be identified based on characteristics of seed coats, floral bracts, and leaf color (Brokaw and Hufford 2011). However, identification can be time consuming and inexact, especially among those unfamiliar with *Mentzelia* sect. *Trachyphytum*. Furthermore, these characters are not available in all developmental stages. Consequently, the hexaploid *M. monoensis* cannot always be reliably distinguished from one of its progenitors, the tetraploid *M. montana,* or the closely related octoploid, *M. albicaulis* (Douglas ex Hook.) Douglas ex Torr. & A Gray (Brokaw and Hufford 2010b, 2011).

Due to these difficulties, a practical technique is necessary in order to effectively identify *M. monoensis*. DNA barcoding has significant potential to facilitate plant identification if prospective sequence regions fit the following criteria (Kress et al. 2005). Sequences should be short enough for dependable DNA extraction, amplification, and sequencing, and must exhibit interspecific divergence. However, the ideal sequence should also have intraspecific consistency (Kress et al. 2005). In plants, popular barcoding candidates have included the internal transcribed spacer region (ITS) and the plastid *trnH-psbA* intergenic spacer (Kress et al. 2005). Nevertheless, among closely related species, these markers are not always variable, resulting in the need to investigate other regions. Previous studies in *Mentzelia* sect. *Trachyphytum* have investigated interspecific relationships using five chloroplast intergenic spacers: *trnH-psbA*, *trnS-trnG*, *trnS-trnfM*, *ndhF-rpL32*, and *rpL32-trnL* (Brokaw and Hufford 2010a, b). Therefore, an objective of this study is to test these regions as potential molecular markers to verify identification of *M. monoensis* and its close relatives for the purpose of ecological comparisons.

Methods

Species Identification

Population sampling. We compared voucher specimens from 70 total populations (Appendix 1), including 24 from *M. monoensis* and 23 from each of the two species most morphologically similar to *M. monoensis*, *M. montana* and *M. albicaulis*. We intensively sampled populations of *M. monoensis* and *M. montana* distributed throughout approximately 1000 km^2 of the Mono Craters volcanic chain in Mono County, California (Fig. 1). We also used specimens from *M. montana* and *M. albicaulis* collected in other parts of Mono County and throughout their ranges in western North America (Fig. 2).

Morphology. Four characters (bract color, bract shape, seed color, and seed coat cell shape) have been previously noted as useful to distinguish *M. monoensis* from *M. montana* and *M. albicaulis* (Brokaw and Hufford 2011). Using the methods of Brokaw and Hufford (2011), we recorded the states from these four morphological characters for all 70 populations in order to compare their consistency with taxon assignments and DNA-based markers. However, in some cases, seed characters had not yet developed on immature vouchers.

DNA isolation and analysis. All cpDNA sequences generated in this study have been deposited with NCBI GenBank (see Appendix 1). DNA extraction was performed for 11 of the vouchers of *M. monoensis M. montana*, and *M. albicaulis* in a previous study by Brokaw and

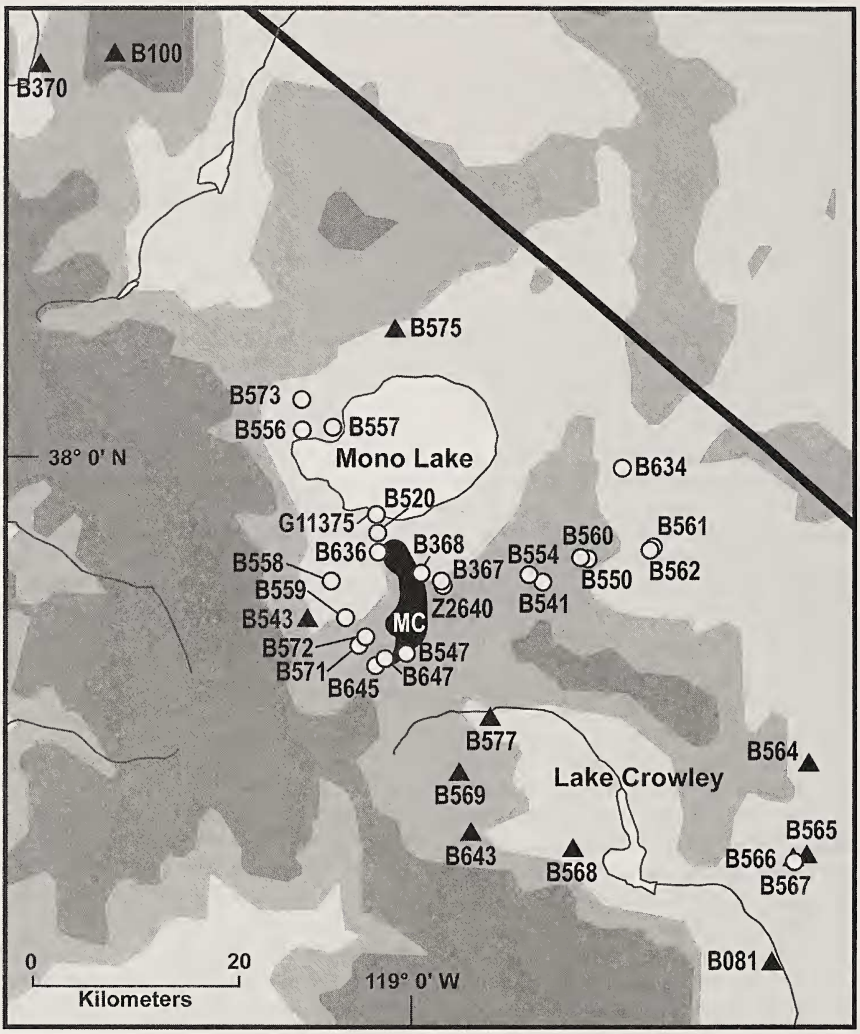

FIG. 1. Sampling map for the Mono Basin region, Mono County, California. Soil and/or genetic sampling locations indicated by open circles (*M. monoensis*) or closed triangles (*M. montana*). MC: location of the Mono Craters indicated in black. Shaded relief layers represent elevations less than 3000 m (light grey), 3000 to 4000 m (medium grey), and greater than 4000 m (dark grey). Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

Hufford (2010b). Total genomic DNA from the 59 new populations was isolated from 10 mg of silica-gel-dried or herbarium specimen leaf material. The plant tissues were ground to a fine powder, and genomic DNA extraction was carried out with an EZNA Plant DNA Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions. The chloroplast spacers *trnH-psbA* and *ndhF-rpL32* were amplified using PCR as described in Marlowe and Hufford (2007). PCR products were sequenced directly.

The PCR protocol for plastid spacers consisted of a 25 μL sample containing 13.8 μL H_2O, 2.5 μL 10× Thermopol Reaction Buffer with 20 mM Mg^{2+} (New England Biolabs, Ipswich, MA), 2.5 μL of each 5 μM primer, 1.5 μL 2.5 mM dNTP, 0.2 μL 5 U/μL Taq polymerase (New England Biolabs), and 2.0 μL diluted DNA template of unknown concentration. PCR conditions in a Biometra thermocycler (Whatman, Göttingen, Germany) included initial denaturation at 94°C for 5 min; followed by 30 cycles at 94°C for 1 min, 55°C for 1 min, and 72°C for 2 min; with a final extension at 72°C for 7 min.

All PCR products were visualized by 1% agarose gel electrophoresis and purified with an EZNA Cycle-Pure Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions, and the purified product was sequenced at the DNA Analysis Facility at Yale University. Sequences were assembled and edited using the program Sequencher version 5.2.4 (Gene Codes Corp., Ann Arbor, MI). New *trnH-psbA* and

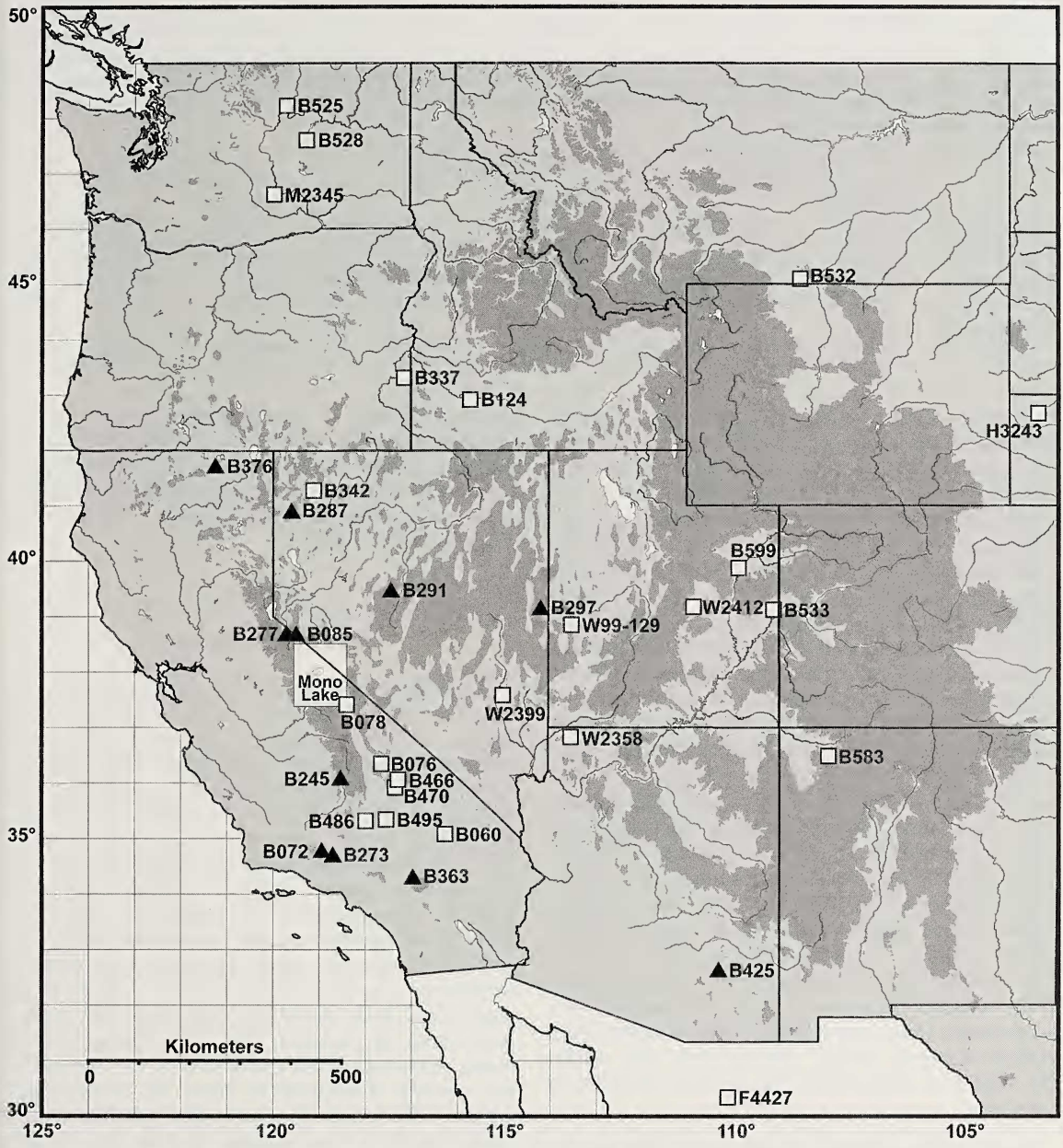

FIG. 2. Sampling map for western North America. Soil and/or genetic sampling locations indicated by closed triangles (*M. montana*) or open squares (*M. albicaulis*). White rectangle encompassing Mono Lake indicates the distribution of *M. monoensis* shown in Fig. 1. Shaded relief layers represent elevations less than 2000 m (light grey) and greater than 2000 m (dark grey). Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

ndhF-rpL32 sequences and those for all five chloroplast intergenic spacers (*trnH-psbA, trnS-trnG, trnS-trnfM, ndhF-rpL32, rpL32-trnL*) from the 11 vouchers of *M. monoensis M. montana*, and *M. albicaulis* previously sequenced by Brokaw and Hufford (2010b) were combined for analysis. Sequences were aligned manually using SE-AL (v2.0a11; Rambaut 1996–2002). Haplotype networks were constructed using TCS version 1.21 (Clement et al. 2000) under the criterion of a parsimony network in which connections have a probability of at least 95%.

Edaphic Characterization

Edaphic data. In 2013, we collected soils from 17 locations within the range of *M. monoensis* representing 15 populations of *M. monoensis*, one population of *M. montana,* and one mixed population of *M. monoensis* and *M. montana*

TABLE 1. INTRASPECIFIC CHARACTER STATE CONSISTENCY OF BRACT COLOR, BRACT SHAPE, SEED COLOR, AND SEED COAT CELL SHAPE IN *M. ALBICAULIS*, *M. MONOENSIS*, AND *M. MONTANA*. For each character, the most common (dominant) of two possible character states and the percentage of specimens exhibiting the dominant state are listed. For bract shape, the less common character state for all species was toothed/lobed. The number of specimens of each species with observable character states is provided; seed color was not reported for seeds darkened during preservation.

	M. albicaulis		*M. monoensis*		*M. montana*	
Character	Dominant state	% consistent	Dominant state	% consistent	Dominant state	% consistent
Bract color	Green	100.00 (n = 23)	Green	69.57 (n = 24)	White base	82.61 (n = 23)
Bract shape	Entire	52.17 (n = 23)	Entire	100.00 (n = 24)	Entire	52.17 (n = 23)
Seed color	Tan	60.00 (n = 10)	Tan	100.00 (n = 21)	Spotted	82.35 (n = 17)
Seed coat cell shape	Pointed	100.00 (n = 15)	Domed	100.00 (n = 22)	Pointed	100.00 (n = 21)

(Appendix 2). In order to compare the edaphic habitats of *M. monoensis* to those of other taxa, we combined this new data with previously collected soils data (Brokaw 2009) from 226 locations representing the distributional and ecological ranges of each of the 24 North American species in *Mentzelia* sect. *Trachyphytum* that have been recognized by Zavortink (1966), Thompson and Roberts (1971), Glad (1976), and Brokaw and Hufford (2010b). The combined data set included samples from 19 populations of *M. monoensis*, 32 populations of *M. montana,* and 32 populations of *M. albicaulis*. Soils were collected as composite samples composed of five 0–15 cm depth soil cores for each locality and sieved to remove particles greater than two mm. Soil diagnostic services were provided by MDS Harris Laboratories (Lincoln, NE). Edaphic data used for comparisons consisted of percent composition of sand, silt, and clay particle sizes, percent soil organic matter (SOM), cation exchange capacity (CEC), pH, concentration of soluble salts (salinity), boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), nitrate-nitrogen (NO_3), phosphorus (P), sulfur (S), and zinc (Zn), from the <2 mm fraction of substrate.

Statistical analyses. Differences in species habitats based on the selected edaphic variables were visualized in multidimensional space using principal components analysis (PCA) of the 243 population soil samples with the CANOCO for Windows software package 4.5.1 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). To test for significant differences between species edaphic niches as represented by groups of population soil samples, an NPMANOVA (Anderson 2001) was conducted using the Euclidean distance matrices created from pair-wise comparisons of population habitat samples. NPMANOVA is a method for multivariate analysis of variance based on Monte-Carlo permutations, that tests for differences in locations of centroids among groups of observations based on the chosen distance measure. NPMANOVA was performed with 9999 unrestricted permutations of the raw data (after centering and standardization) using the software package PAST 2.17 (Hammer et al. 2001).

RESULTS

Species Identification

Morphology. Seed coat cell shape was the only morphological character with uniform states within all three species (Table 1). *Mentzelia monoensis* has domed seed coat cells, and *M. montana* and *M. albicaulis* have pointed seed coat cells (see Brokaw and Hufford 2011). All specimens of *M. monoensis* had entire bracts and tan seeds, but both *M. montana* and *M. albicaulis* are polymorphic for these characters, and *M. monoensis* is polymorphic for bract color. Only 57 of the 70 voucher specimens (81%) had sufficiently mature seeds that could be used to determine seed coat cell shape, and bract characters alone could not distinguish *M. monoensis* from *M. montana* and *M. albicaulis* in all cases. Although fresh specimens of *M. monoensis* can usually distinguished from *M. montana* by subtle differences in leaf color (Brokaw and Hufford 2011), this character was not reliable for preserved specimens and our final determinations of species identities were not based on morphology if seed coat cell shape could not be determined.

DNA isolation and analysis. The *ndhF-rpL32* intergenic spacer was determined to be the most useful genetic marker for identification of *M. monoensis*. Preliminary analyses of three of the five chloroplast spacers (*trnS-trnG*, *trnS-trnfM*, *rpL32-trnL*) revealed that *M. monoensis* lacked unique variation in these regions that could be used for discrimination from *M. montana* and *M. albicaulis*; no further sequencing was performed using these markers. Some populations of *M. monoensis* (B367, B547, Z2640) were found to

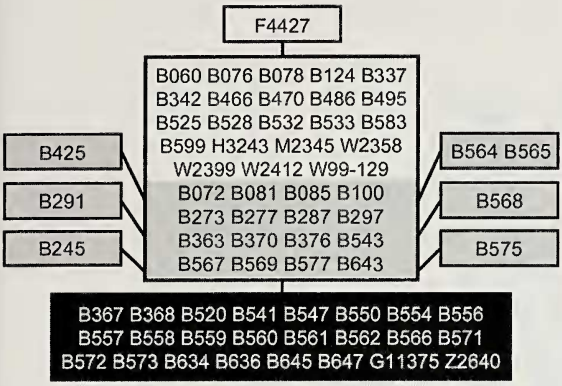

FIG. 3. Haplotype network of *ndhF-rpL32* sequences generated in TCS. Rectangles correspond to sampled haplotypes from *M. monoensis* (black), *M. montana* (grey), and *M. albicaulis* (white). Lines connecting haplotypes represent a single substitution. Sample labels represent abbreviated voucher collection numbers (see Appendix 1).

contain a unique nucleotide substitution in *trnH-psbA*. However, subsequent sampling determined that this haplotype was limited to populations near the type locality of *M. monoensis* (including collections from as early as 1966 and as recently as 2009) but not present in most populations of *M. monoensis*. Therefore, because many populations of *M. monoensis* have the same *trnH-psb A* haplotype as *M. montana* and *M. albicaulis*, sequencing of *trnH-psbA* was also discontinued. The most common haplotype of *ndhF-rpL32* was shared by most specimens of *M. montana* and *M. albicaulis*; six haplotypes in *M. montana* and one additional haplotype in *M. albicaulis* each differed from the most common haplotype by a single substitution (Fig. 3). None of the haplotypes from *M. montana* and *M. albicaulis* were shared by *M. monoensis*. All specimens of *M. monoensis* had an identical *ndhF-rpL32* haplotype that was unique to *M. monoensis* and differed from the most common haplotype in and *M. albicaulis* by a single nucleotide substitution of a C-G pair (present in *M. monoensis*) for an A-T pair (present in *M. montana* and *M. albicaulis*). This transversion in *ndhF-rpL32* also distinguishes *M. monoensis* from all other species in *Mentzelia* sect. *Trachyphytum* analyzed by Brokaw and Hufford (2010b). Further, among vouchers in this study that had mature seeds, this single nucleotide polymorphism (SNP) showed a perfect correlation with seed coat cell shape. Thus this C-G/A-T SNP has become the most reliable character currently available for identification of herbarium specimens of *M. monoensis* at all stages of development. Therefore, specimens in this study lacking mature seeds were identified using this marker if chromosome counts were not available.

Edaphic Characterization

Principal components analysis suggests that the edaphic niche of *M. monoensis* is extreme with respect to those of other species, including the progenitors of *M. monoensis* (Fig. 4). The first two principal components account for 52.6% of total variance, with 32.3% on the first principal component and 20.3% on the second. The first principal component (PC1) is positively correlated with percent sand (vector loading = 0.71) and strongly negatively correlated with cation exchange capacity (vector loading = 0.94) and concentration of soluble salts (vector loading = 0.91). The second principal component (PC2) is positively correlated with extractable phosphorus (vector loading = 0.79), zinc (vector loading = 0.76), manganese (vector loading = 0.74), and iron (vector loading = 0.73) and soil organic matter (vector loading = 0.72) and negatively correlated with pH (vector loading = 0.70). These results are summarized in a biplot of the first two principal components (Fig. 4). In the biplot of PC1 and PC2 only five populations of other species including one from *M. montana* and two from *M. albicaulis* are positioned within the two dimensional envelope representing all 19 sampled populations from *M. monoensis*. Populations from *M. monoensis* represented the seven highest sample values on PC1. The three samples with highest overall values on PC1 (B647, B572, B547) were also among those collected nearest the Mono Craters chain (Fig. 1); a fourth of these nearest samples (B636) was collected from a recently burned site and had the lowest PC1 value of any *M. monoensis* soil. Three of the six *M. monoensis* samples with lowest PC1 scores (B573, B556, B557) were collected on or nearest Black Point, a basaltic cinder cone on the northwestern shore of Mono Lake, and the remaining two lowest (B645 and B562) were collected along the disturbed margins of paved highways near the southwestern and northeastern edges of the *M. monoensis* range respectively (Fig. 1). The southeastern most sampled population of *M. monoensis* (B566) was nearly 30 km from the nearest known population of *M. monoensis* and had an intermediate PC1 value with respect to other *M. monoensis* samples. At this disjunct location, *M. monoensis* was found growing in a mixed population with *M. montana* (B567), representing the highest PC1 sample value for *M. montana* in this study. In contrast to PC1, populations from *M. monoensis* did not have extreme values on PC2. Values from *M. monoensis* samples fell completely within and spanned most of the range of values for other species in *Mentzelia* sect. *Trachyphytum*, although the burned B636 site was a high outlier on PC2 compared to other *M. monoensis* samples. Differences between sets of soil samples grouped by species were tested with

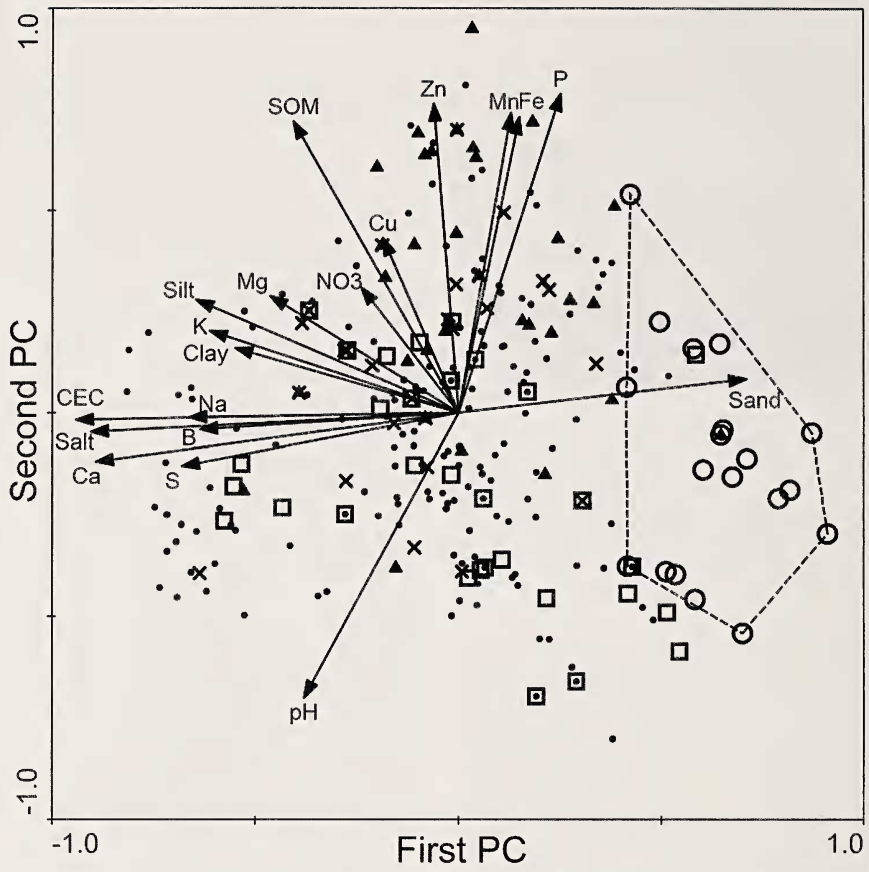

FIG. 4. Biplot for the first two principal components from principal components analysis (PCA) of soil chemistry and texture data for 243 assayed soil samples; the first PC represents 32.3% of total variance; the second PC represents 20.3% of total variance; arrows represent direction and magnitude of loading for soil variables on the principal component axes; open circles and dashed envelope represent soils from *M. monoensis*; closed triangles represent *M. montana*; open squares represent *M. albicaulis*; X-marks represent *M. dispersa*; points represent all other North American species in *Mentzelia* sect. *Trachyphytum*. Symbols: CEC = cation exchange capacity; N03 = nitrate; SOM = soil organic matter.

NPMANOVA. The NPMANOVA showed that the sampled soils of *M. monoensis* were significantly different ($P < 0.0001$) from those of all other North American species in *Mentzelia* sect. *Trachyphytum*, including *M. montana* and *M. albicaulis*.

DISCUSSION

Mentzelia monoensis is a unique species that can be reliably distinguished from its closest relatives with a simple genetic marker. The distinct hexaploid karyotype of *M. monoensis* has been recognized for over 50 yr (Zavortink 1966). However, its morphology, geography, and evolution had not been thoroughly investigated until recently due in part to the lack of reliable morphological characters for identification (Brokaw and Hufford 2010b, 2011). In addition to broadening our understanding of the morphological and geographic variation in *M. monoensis*, recent work has suggested a unique origin story; *M. monoensis* is the only allopolyploid thought to have formed through a hybridization involving the two major subclades within *Mentzelia* sect. *Trachyphytum*, "Affines" and "Trachyphyta," via the progenitors *M. dispersa* (diploid or tetraploid) and *M. montana* (tetraploid) respectively (Brokaw and Hufford 2010b). With the discovery of unique variation in the *ndhF-rpL32* intergenic spacer for use as a genetic barcode for *M. monoensis*, the reliability of identification is now sufficient to support ecological and biogeographic investigations based on fresh and preserved voucher specimens at all developmental stages. Although *ndhF-rpL32* has not proven to be sufficiently variable to provide unique haplotypes for some species, including *M. montana* and *M. albicaulis*, the simplicity of the unique character (a single nucleotide transversion) distinguishing *M. monoensis* from other species will allow for more rapid and cost effective identifi-

cation of candidate specimens through the development of allele specific PCR protocols (Gaudet et al. 2007, 2009). The need to use molecular technologies for reliable identification can be a burdensome addition to ecological investigations, but reliance on morphology-based taxonomy has resulted in the underrepresentation of species richness in nature and obscured insight into ecology and evolution (Soltis et al. 2007). Prior to the availability of molecular and cytological evidence this bias has concealed the unique ecological status of *M. monoensis* revealed by this study.

Now with a reliable method for identification, we suggest that the apparent endemism of *M. monoensis* is most likely the result of edaphic specialization for the volcanic substrates of the Mono Basin rather than simply a byproduct of misidentification. An NPMANOVA based on measured soil characteristics suggests that the edaphic niche of *M. monoensis* is significantly different from those of all other species in *Mentzelia* sect. *Trachyphytum*. According to principal components analysis of these data (Fig. 4), the edaphic niche of *M. monoensis* is also one of the most extreme in *Mentzelia* sect. *Trachyphytum*. *Mentzelia monoensis* is found in soils that are generally coarser in texture and lower in cation exchange capacity and plant available nutrients than those of other species in its section. These findings are consistent with the chemical content and weathering rates of silica-rich rhyolites deposited in the Mono Basin during the most recent eruptions of the Mono Craters (Patten et al. 1987; Bailey 2004; Wolff-Boenisch 2004, 2006). In agreement with an edaphic explanation for the distribution of *M. monoensis*, the tephra fields of the Long Valley Volcanic Chain differ substantially in chemical composition from soils from comparable elevation and vegetation types in the Great Basin (Patten et al. 1987), and *M. monoensis* is primarily limited to soils derived from these deposits. Although experimental data on *M. monoensis* and related species grown under reciprocal conditions could yield more conclusive insights about the role of edaphic specialization in geographic isolation, the hypothesis of edaphic constraints is consistent with observed physical and chemical gradients in the Mono Craters tephras. For example, the soil samples from *M. monoensis* in this study with the most extreme values with respect to other species in *Mentzelia* sect. *Trachyphytum* are closest to the Mono Craters, and those with the least extreme values are near the edges of the *M. monoensis* distribution. The positions of these gradients are explained by the observation that eruptions deposit the deepest, coarsest tephra nearest the Mono Craters (Bailey 2004).

As a putative Mono County endemic, *M. monoensis* has a unique geographic distribution in *Mentzelia* sect. *Trachyphytum*. Most species in *Mentzelia* sect. *Trachyphytum* have at least a portion of their distributions in southern California, suggesting that southern California is either an ancestral or refugial region for *Mentzelia* sect. *Trachyphytum* as a whole (Brokaw et al. 2011). Of the few examples of species distributed entirely outside of southern California, all are species that have been associated with unusual soil conditions: *M. crocea* Kellogg and *M. lindleyi* Torr & A. Gray with serpentine soils (Zavortink 1966), *M. mollis* M. Peck and *M. packardiae* J. B. Glad with saline-sodic soils (Glad 1976), *M. thompsonii* J. B. Glad with calcareous soils (Brokaw et al. 2011), and *M. monoensis* with nutrient deficient soils (Brokaw and Hufford 2011). Although explanations of endemism likely involve a combination of historical, genetic, and environmental factors (Stebbins 1980), this pattern suggests that adaptation to localized edaphic conditions has played a major role in the distributions of these disjunct endemics. Further, the narrow distributions of other endemic plant species in the Mono Basin tephra fields (Sugden 1985) provide support for the role of the Mono Craters in the repeated creation of edaphic endemics, including *M. monoensis*.

Edaphic factors have long been regarded as potential drivers of plant diversification (Stebbins 1942; Kruckeberg 1986; Rajakaruna 2004). Because *M. monoensis* is a relatively young neoendemic, it is likely that the edaphic specialization associated with its narrow distribution resulted from and promoted its establishment as a new species. Although polyploidization has often been considered a form of instant, sympatric speciation in the context of biological species concepts (Coyne and Orr 2004), the subsequent establishment of a self-sustaining polyploid population can be threatened by reproductive competition from sympatric progenitors (Hagberg and Ellerstrom 1959; Levin 1975). Factors that may alleviate this minority cytotype disadvantage include self-pollination (Levin 1975), stochastic effects (Rausch and Morgan 2005), and adaptive/ecological advantages (Leitch and Leitch 2008, Ramsey 2011). *Mentzelia monoensis*, like other species in *Mentzelia* sect. *Trachyphytum*, is capable of substantial self-fertilization (Zavortink 1966). However, predominant selfing alone cannot explain successful establishment in the absence of chance events and/or ecological divergence (Levin 1975, Felber 1991). Adaptation has been used to explain the successful establishment of new cytotypes either following stochastic events (Lewis 1961, 1966) or as a result of novel traits caused by the polyploidization itself (Ramsey 2011). A critical factor in both explanations is that spatial isolation of new polyploids from the source populations is required and must be maintained until the polyploid population is

capable of eliminating or coexisting with migrants with other cytotypes (Lewis 1961, 1966). Based on these premises, the simplest explanation for the establishment of *M. monoensis* is that the new hexaploid population(s) multiplied in isolation from diploid and tetraploid progenitors and relatives after stochastic dispersal event(s) fortuitously placed the first hexaploid seed(s) in the uncolonized ejecta from the recently formed Mono Craters. This scenario does not require that progenitor species be incapable of colonizing the same habitats. Most species in *Mentzelia* sect. *Trachyphytum* exhibit spotty, stochastic colonization patterns of populations interspersed among many suitable but unused habitats (personal observation). This suggests that the lucky placement of a new polyploid seed in an uninhabited location may be the first and most critical step in establishment. According to this hypothesis, the eruptions of the Mono Craters may have been more important as mechanisms for providing new cleared space for colonization than for the chemical characteristics of their deposits. However, following successful dispersal and population establishment, it has been suggested that polyploidization may confer novel traits and/or more rapid responses to natural selection in ways that facilitate specialization for the new habitats (Leitch and Leitch 2008, Ramsey 2011). Once establishment is secured, an additional adaptive advantage to the neopolyploid is the postzygotic suppression of gene flow that might otherwise impede ecological divergence from progenitors and specialization to new substrates (Lewis 1962, 1966). In agreement with this assertion of suppressed gene flow, controlled crosses between *M. monoensis* and other species in *Mentzelia* sect. *Trachyphytum* have revealed strong reproductive isolation (Zavortink 1966). In crosses with hexaploids, *M. monoensis* either produced a small number of nonviable seeds or failed to produce seeds entirely, and all crosses in *Mentzelia* sect. *Trachyphytum* involving mixed ploidy levels resulted in 99–100% reduction in seed production and no germination (Zavortink 1966). Together these genetic and biogeographic circumstances might provide neopolyploids with an evolutionary trajectory very different from that of the parental species (Lewis 1966). Thus, morphologically cryptic differences in karyotype could have important ecological consequences (Soltis et al. 2007).

Although escape from endemism caused by edaphic specialization has been inferred to be rare (Anacker 2011), it might be premature to conclude that *M. monoensis* is an "evolutionary dead-end" (Anacker 2011, p. 374). Ongoing adaptive potential has been inferred for both habitat specialists and polyploid species (Nosil and Mooers 2005; Otto 2007). Stebbins (1942) first proposed that neoendemics become constrained to a narrow distribution through loss of genetic variation by genetic drift and/or natural selection, and this expectation of genetic depletion in *M. monoensis* is supported by sequence data from *ndhF-rpL32* that suggests *M. monoensis* has lower cpDNA diversity than *M. montana* and *M. albicaulis*. However, these data do not take into account the diversifying effects of allopolyploidization on the nuclear genome of *M. monoensis* (Otto 2007; Leitch and Leitch 2008). Further support for the potential of *M. monoensis* to acquire a different or more generalized niche may be gained from the observation that many of the *M. monoensis* habitats with the least extreme chemical characteristics had been subjected to burning or mechanical disturbance. This suggests that *M. monoensis* is capable of inhabiting a wider variety of soil conditions when competition is reduced through disturbance. Other edaphic endemics in *Mentzelia* sect. *Trachyphytum*, including *M. mollis* and *M. packardiae*, have similar patterns of distribution on stressful and disturbed soils and have even been successfully grown in standard potting soil (Brokaw, personal observation), suggesting that these unusual substrates may act as a refuge from competition rather than providing essential chemical resources. Finally, *M. monoensis* has been found in mixed populations with both *M. montana* and the diploid *M. congesta* Torr. & A. Gray (Brokaw, personal observation), suggesting that at least temporary coexistence is possible with other species in *Mentzelia* sect. *Trachyphytum*, albeit usually at the edges of the *M. monoensis* range.

It is also possible that further range expansion will be achieved by *M. monoensis* without any significant adaptive change. Although the historical explanation that neoendemics are narrowly distributed simply because they have had insufficient time for dispersal (Willis 1922) has been thoroughly criticized (Stebbins 1980), species age may play a major role in the likelihood of improbable events such as long distance dispersal to islands of habitat suitable for edaphic specialists (MacArthur and Wilson 1967). Although still within the boundaries of Mono County, one population of *M. monoensis* (B566) has already been found nearly 30 km southeast of the next closest population. No other known populations of *M. monoensis* are separated from their nearest neighbors by more than 10 km. However, the soil properties from this disjunct location do not suggest a new or marginal habitat. Rather, the B566 site is still part of the same Long Valley Volcanic Field that contains Mono Craters (Bailey 2004), and the chemical and physical properties from this site fell near the middle of the distribution of properties from soils collected within the contiguous *M. monoensis* range. *Mentzelia monoensis* has not been found in the

intervening region separating the B566 site from the contiguous *M. monoensis* range because the Glass Mountain Ridge is higher in elevation and lacks the deep ash deposits found both at B566 and surrounding the Mono Craters (Bailey 2004). For the same reasons, *M. monoensis* has also not been found on the steep peaks in the heart of the Mono Craters chain. The occurrence of the B566 population suggests that *M. monoensis* can colonize disjunct habitats if the soils are suitable, but substantial time might be necessary for additional range expansions through low frequency dispersals when suitable sites (if they exist) occur at great distances.

Nevertheless, the future of any neopolyploid is precarious due to its initially narrow distribution (Leitch and Leitch 2008), and the fate of *M. monoensis* remains unclear. We have not identified any imminent threats to the persistence of *M. monoensis*, and, where it is found, *M. monoensis* is often abundant and tolerates or responds favorably to intermediate levels of disturbance associated with road maintenance, hillside erosion, and fire (Brokaw, personal observation). However, *M. monoensis* is an annual species that presumably requires favorable conditions for germination and growth that are vulnerable to climate change. Interestingly, some edaphic endemics in *Mentzelia* sect. *Trachyphytum*, including *M. mollis* and *M. thompsonii*, appear to be paleoendemics with disjunct distributions caused by their successful persistence on unusual substrates in the face of shifting conditions during episodes of prehistoric climate change (Glad 1975; Brokaw et al. 2011). However, adaptation models suggest that extinction rather than evolution is likely if environmental conditions change too rapidly (Hoffman and Sgró 2011).

The Mono Lake region has been an area of concern for conservationists as a result of unnatural diversion of water pathways and the resulting changes in aquatic ecology that have been further exacerbated by human induced climate change (Patten et al. 1987; Wiens et al. 1993; Millar and Woolfenden 1999). However, the same geological forces that created Mono Lake have also generated a unique edaphic environment throughout the semi-arid terrestrial communities of the Mono Basin (Patten et al. 1987; Bailey 2004). Although a small number of plants endemic to the Mono Basin have been discovered (Sugden 1985), it is possible that other undiscovered endemics are present. Finally, it must be acknowledged that we cannot be fully confident that we have identified the entire geographic range circumscribing the putative endemism of *M. monoensis*. However, we expect that any major range extensions would represent narrow disjunct distributions likely associated with similar edaphic conditions. Regardless of any such discoveries, observations from this study confirm that *M. monoensis* is a unique, albeit cryptic, component of the remarkable Mono Basin ecosystem.

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APPENDIX 1

Voucher information and GenBank accessions for specimens in this study. Missing data are indicated with an en dash (–). **Voucher code:** Voucher *collector* and *collection number*, deposition herbarium acronym, latitude, longitude, elevation in meters; GenBank accession numbers for *ndhF-rpL32*, *trnH-psbA*. ACU: Abilene Christian University Herbarium; LA: University of California, Los Angeles Herbarium; UT: Utah Museum of Natural History, Garrett Herbarium; WS: Marion Ownbey Herbarium.

Mentzelia albicaulis

B060: *Brokaw 060* (WS), 35.06260, −116.28833, 356 m; KM043532, –. **B076:** *Brokaw 076* (WS), 36.30335, −117.63695, 1631 m; KM043533, –. **B078:** *Brokaw 078* (WS), 37.15513, −118.28947, 1236 m; KM043534, –. **B124:** *Brokaw 124* (WS), 42.90667, −115.69203, 762 m; KM043535, –. **B337:** *Brokaw 337* (WS), 43.28265, −117.25745, 1177 m; FJ917857, FJ918127. **B342:** *Brokaw 342* (WS), 41.22359, −119.07072, 1391 m; KM043536, –. **B466:** *Brokaw 466* (WS), 35.98656, −117.34270, 661 m; KM043537, –. **B470:** *Brokaw 470* (WS), 35.89770, −117.33201, 704 m; KM043538, –. **B486:** *Brokaw 486* (WS), 35.31596, −118.05270, 758 m; KM043539, –. **B495:** *Brokaw 495* (WS), 35.36298, −117.63688, 1185 m; KM043540, –. **B525:** *Brokaw 525* (WS), 48.21440, −119.70982, 270 m; KM043541, –. **B528:** *Brokaw 528* (WS), 47.62568, −119.34213, 522 m; KM043542, –. **B532:** *Brokaw 532* (WS), 45.05924, −108.66726, 1381 m; KM043543, –. **B533:** *Brokaw 533* (WS), 39.03924, −109.28689, 1382 m; KM043544, –. **B583:** *Brokaw 583* (ACU), 36.53905, −107.95961, 1938 m; KM043545, –. **B599:** *Brokaw 599* (ACU), 39.94981, −109.90137, 1563 m; KM043546, –. **F4427:** *Fishbein 4427* (WS), 30.36, −110.60, 950 m; FJ917858, FJ918128. **H3243:** *Hufford 3243* (WS), 42.58, −103.40, 1350 m; FJ917859, FJ918129. **M2345:** *Mastrogiuseppe 2345* (WS), 46.91, −119.98, 150 m; FJ917860, FJ918130. **W2358:** *Windham 2358* (UT), 36.83083, −113.573056, 1487 m; KM043547, –. **W2399:** *Windham 2399* (UT), 37.59788, −115.054263, 1471 m; KM043548, –. **W2412:** *Windham 2412* (UT), 39.20328, −110.86160, 1738 m; KM043549, –. **W99–129:** *Windham 99–129* (UT), 38.83605, −113.515268, 1769 m; KM043550, –.

Mentzelia monoensis

B367: *Brokaw 367* (WS), 37.89570, −118.97472, 2257 m; FJ917907, FJ918178. **B368:** *Brokaw 368* (WS), 37.90589, −118.98978, 2118 m; KM043492, KM043552. **B520:** *Brokaw 520* (WS), 37.92793, −119.04869, 2118 m; FJ917908, FJ918179. **B541:** *Brokaw 541* (ACU), 37.89570, −118.97472, 2257 m; KM043493, –. **B547:** *Brokaw 547* (ACU), 37.82022, −119.00142, 2354 m; KM043494, KM043551. **B550:** *Brokaw 550* (ACU), 37.89451, −118.85307, 2456 m; KM043495, –. **B554:** *Brokaw 554* (ACU), 37.89023, −118.86738, 2481 m; KM043496, KM043553. **B556:** *Brokaw 556* (ACU), 38.02101, −119.13085, 1975 m; KM043497, KM043554. **B557:** *Brokaw 557* (ACU), 38.02763, −119.08554, 1972 m; KM043498, KM043555. **B558:** *Brokaw 558* (ACU), 37.88666, −119.09028, 2103 m; KM043499, KM043556. **B559:** *Brokaw 559* (ACU), 37.86439, −119.08492, 2161 m; KM043500, KM043557. **B560:** *Brokaw 560* (ACU), 37.89059, −118.78930, 2243 m; KM043501, KM043558. **B561:** *Brokaw 561* (ACU), 37.92131, −118.70541, 2008 m; KM043502, KM043559. **B562:** *Brokaw 562* (ACU), 37.91792, −118.71134, 2048 m; KM043503, KM043560. **B566:** *Brokaw 566* (ACU), 37.63795, −118.63873, 2247 m; KM043504, KM043561. **B571:** *Brokaw 571* (ACU), 37.84638, −119.06704, 2236 m; KM043505, KM043562. **B572:** *Brokaw 572* (ACU), 37.84789, −119.06490, 2225 m; KM043506, KM043563. **B573:** *Brokaw 573* (ACU), 38.05379, −119.12708, 2054 m; KM043507, KM043564. **B634:** *Brokaw 634* (ACU), 37.98300, −118.73704, 2101 m; KM043508, –. **B636:** Brokaw 636 (ACU), 37.91346, −119.04558, 209 m; KM043509, –. **B645:** *Brokaw 645* (ACU), 37.80689, −119.04564, 2391 m; KM043510, –. **B647:** *Brokaw 647* (ACU), 37.81412, −119.03428, 2350 m; KM043511, –. **G11375:** *Grable 11375* (WS), 37.94, −119.05, 1950 m; KM043512, –. **Z2640:** *Zavortink 2640* (LA), 37.89570, −118.97472, 2250 m; FJ917909, FJ918180.

Mentzelia montana

B081: *Brokaw 081* (WS), 37.50808, −118.58355, 1770 m; KM043514, KM043566. **B085:** *Brokaw 085* (WS), 38.64287, −119.54777, 1605 m; FJ917910, FJ918181. **B100:** *Brokaw 100* (WS), 38.34870, −119.36365, 2290 m; KM043515, KM043567. **B245:** *Brokaw 245* (WS), 35.97818, −118.54830, 1544 m; KM043526, KM043568. **B273:** *Brokaw 273* (WS), 34.77523, −118.97, 2436 m; KM043516, KM043569. **B277:** *Brokaw 277* (WS), 38.67768, −119.73907, 1730 m; FJ917930, FJ918201. **B287:** *Brokaw 287* (WS), 40.88940, −119.61382, 1762 m; KM043517, KM043570. **B291:** *Brokaw 291* (WS), 39.23950, −117.77805, 1902 m; KM043527, KM043571. **B297:** *Brokaw 297* (WS), 39.02630, −114.25310, 2463 m; KM043518, –. **B363:** *Brokaw 363* (WS), 34.26765, −116.94305, 2071 m; KM043519, –. **B370:** *Brokaw 370* (WS), 38.34375, −119.43793, 2193 m; FJ917931, FJ918202. **B376:** *Brokaw 376* (WS), 41.66470, −121.25054, 1274 m; KM043520, –. **B425:** *Brokaw 425*

(WS), 32.53211, −110.71064, 1484 m; FJ917911, FJ918182. **B543:** *Brokaw 543* (ACU), 37.85869, −119.12144, 2274 m; KM043521, KM043572. **B564:** *Brokaw 564* (ACU), 37.72669, −118.59816, 2210 m; KM043528, KM043573. **B565:** *Brokaw 565* (ACU), 37.65005, −118.61573, 2232 m; KM043529, KM043574. **B567:** *Brokaw 567* (ACU), 37.63795, −118.63873, 2247 m; KM043522, KM043575. **B568:** *Brokaw 568* (ACU), 37.62344, −118.81859, 2136 m; KM043530, KM043576. **B569:** *Brokaw 569* (ACU), 37.70919, −118.95180, 2313 m; KM043523, KM043577. **B575:** *Brokaw 575* (ACU), 38.12413, −119.03270, 2140 m; KM043531, KM043578. **B577:** *Brokaw 577* (ACU), 37.74922, −118.93038, 2215 m; KM043524, KM043579. **B643:** *Brokaw 643* (ACU), 37.64034, −118.93877, 2313 m; KM043525, –.

Appendix 2

Soil Chemistry Data Collected During This Study.

Sand, Silt, Clay = percent composition of sand, silt, and clay. SOM = percent soil organic matter. CEC = cation exchange capacity (meq/100 g). Salinity = salt concentration estimated as soil electrical conductivity (dS m^{-1}). Elements and compounds are measured in parts per million of the <2 mm fraction of substrate. Vouchers codes represent collection numbers for J. M. Brokaw. Populations of *Mentzelia montana* (B567 and B643) are indicated by an asterisk (*); all other vouchers are *M. monoensis*. B566 and B567 are from a mixed population of *M. monoensis* and *M. montana*, are represented by a single composite soil sample. All other soil chemistry data are reported by Brokaw (2009).

Vouchers	Sand	Silt	Clay	SOM	CEC	pH	Salinity	B	Ca	Cu	Fe	K	Mg	Mn	Na	NO_3	P	S	Zn
B547	96	4	0	1	1.7	6.3	0.08	0	209	1.1	5.8	32	18	0.8	3	4	18	5	0.7
B550	92	8	0	1.3	2	6.9	0.08	0.1	280	0.8	4.8	70	43	2.7	6	3	23	6	0.5
B556	98	2	0	1.6	4.1	6.6	0.13	0.2	698	1.1	16.5	120	35	4.6	9	7	53	6	2.5
B557	100	0	0	0.7	4.4	7.7	0.13	0.6	535	0.5	16.6	354	84	1.8	34	4	15	7	0.3
B558	94	6	0	1.3	2.7	6.5	0.1	0.1	316	0.8	19.2	127	46	1.9	4	5	27	5	4
B559	90	10	0	0.7	2.3	5.8	0.09	0.1	204	0.8	10	67	39	3.6	6	4	14	5	0.6
B560	98	2	0	1.1	1.4	6.2	0.07	0.1	140	0.7	8.3	51	18	2	2	3	10	4	0.4
B562	100	0	0	1.3	4.4	8.1	0.16	0.3	676	0.9	6.5	102	70	2.4	42	8	6	7	0.6
B572	100	0	0	1.7	2.4	5.9	0.09	0.1	257	0.7	17	50	22	4.3	3	4	18	5	0.8
B573	98	2	0	0.5	8.8	8.4	0.16	0.2	1703	1.4	7.5	39	22	2.5	6	3	7	9	1.1
B634	100	0	0	1	3	8	0.09	0.2	504	0.7	4.4	66	39	1.7	5	3	7	5	0.4
B636	92	8	0	3.4	6.1	5.5	0.16	0.2	611	1.5	30.3	88	50	8.3	7	10	40	7	3.5
B645	94	6	0	1.3	4.5	7.1	0.14	0.1	646	1.5	13.4	94	97	3.3	46	4	16	5	1.6
B647	98	2	0	0.7	1.1	6.3	0.07	0	83	0.7	4.6	40	25	0.8	5	3	18	5	0.5
B566, B567*	86	14	0	1.7	1.6	6.2	0.07	0.1	162	1.1	5.7	78	22	1.8	4	3	11	4	0.9
B643*	88	12	0	2.2	8.3	5.7	0.2	0.1	621	1	32.5	145	92	3.9	20	12	171	8	2.4